The Nerves of the Thoracic Segments of the Larva of *Prodenia litura* (Lepidoptera: Noctuidae)

J. Bahadur and B. B. L. Srivastava
School of Studies in Zoology, Vikram University, Ujjain (India)

Abstract. The nervous system of the thoracic segments of the larva of *Prodenia litura* is described. The dorsal and transverse nerves remain connected to each other at three points through three connectives. But in the prothoracic segment, there is no transverse nerve, so that the dorsal nerve establishes a connection with subconnective nerve by a plexus. Ordinarily no connection is found between the dorsal and ventral nerve but in the prothoracic segment, such a connection is established at one point.

INTRODUCTION

The studies on the nervous system started with the work of Lyonet (1762). Since then many aspects of it have been dealt with. Du Porte (1915) described the nervous system in *Sphida* and Ruckes (1919) studied the innervation of the male genital organs in certain lepidopterans. However, the real work on the nerve pattern started with Maki (1936) who described it in the alderfly, *Chauliodes formosanus*. Nesbitt (1941) studied the nerve patterns in Orthoptera and other related orders. Schmitt (1954, 1959) studied the nervous system of cervicothoracic and the pregenital abdominal segments in some orthopterans. With these studies it was realized that there exists a basic segmental nerve pattern in insects. Whether such a homology can be traced in widely separated orders as Orthoptera and Lepidoptera, is yet to be seen. Libby (1959, 1961), however, investigated the nerve pattern of certain abdominal segments of the larva and adult of the moth, *Hyalophora cecropia* and tried to establish homology with other insect nerve patterns. The short review shows that the thorax has not been tackled so far in detail. To fill up this lacuna and to establish how far there exists a basic homology with the thorax of other insect orders, the authors undertook a very detailed study of the nerves of the thoracic segments of the larva of *Prodenia litura*.

MATERIAL AND TECHNIQUES

The full grown larvae were directly collected from the cabbage fields and kept in the laboratory. For the studies on the distribution of the nerves, 1% methylene blue in normal salt solution was injected into the body cavity of the larva. After a few hours, the insect was etherized and dissected in normal saline (0.65%). Sometimes, instead of injecting the solution into the body cavity, the dye was directly poured over the dissected animal and allowed to stay for 2 to 4 hours to secure better staining of finest motor nerves. Further dissection was done in normal saline. To destain the adjoining tissues, acid water was sometimes used. Normally, all the nerves of a particular segment

could not be traced in one day and hence the dissection used to be kept in normal saline with a few drops of formalin. In such preservation, the blue colour of the nerves disappears but they remain quite distinct because of the milky white appearance which they attain. All the dissections were carried out under the stereoscopic binocular microscope in artificial light. The diagrams are purely diagrammatic.

OBSERVATIONS

The thorax is composed of three segments with their ganglia. The prothoracic ganglion remains connected to the suboesophageal ganglion by a pair of stout but short connectives which lie free throughout their entire length. The connectives between the other ganglia lie united anteriorly for about one fifth of the distance and then diverge gradually, continuing their course separately until they enter the anterior border of the succeeding ganglion. The two separated connectives enclose between them some space within which the diagonal muscles cross each other near their point of insertion. The enclosed space is smaller in the prothoracic segment but larger in the other two segments.

NERVES OF THE PROTHORACIC GANGLION (Fig. 1)

The prothoracic ganglion gives rise to two pairs of lateral nerves and a pair of subconnective nerves. The lateral nerves are designed as the dorsal and the ventral nerves. From the median portion of the ganglion arises a pair of subconnective nerves. *The Dorsal Nerve*: The dorsal nerve (DN) leaves the ganglion and runs obliquely outwards and upwards over the ventral median muscles and ventral internal lateral muscles to reach the subconnective nerve (SN) with which it forms a plexus (px). It then sharply bends downwards, passes over the ventral internal muscles and extends to a considerable distance, giving branches at intervals. The first branch (ID) arises over the ventral internal longitudinal muscle and divides into two branches; the inner branch (a) passes downwards and curves slightly inwards and bifurcates to innervate the tracheae and the tracheoles. The outer branch (b) curves and bifurcates into b′ and b″. Whereas the former innervates the ventral internal lateral longitudinal muscle, the latter meets the longitudinal nerve of the dorsum (LND) which extends from the head up to the intersegmental fold of this segment. The main dorsal nerve proceeds further and after a short distance, besides receiving the sixth branch (6V) of the ventral nerve, itself gives rise to the second branch (2D). This branch divides into a number of branches to innervate the adjoining neck muscles and the tracheae. The third branch (3D) proceeds dorsally and gives rise to a number of branches which again innervate the various muscles and integument of the neck region. The fourth branch (4D) innervates the tergosternal muscle. The main dorsal nerve ulti-

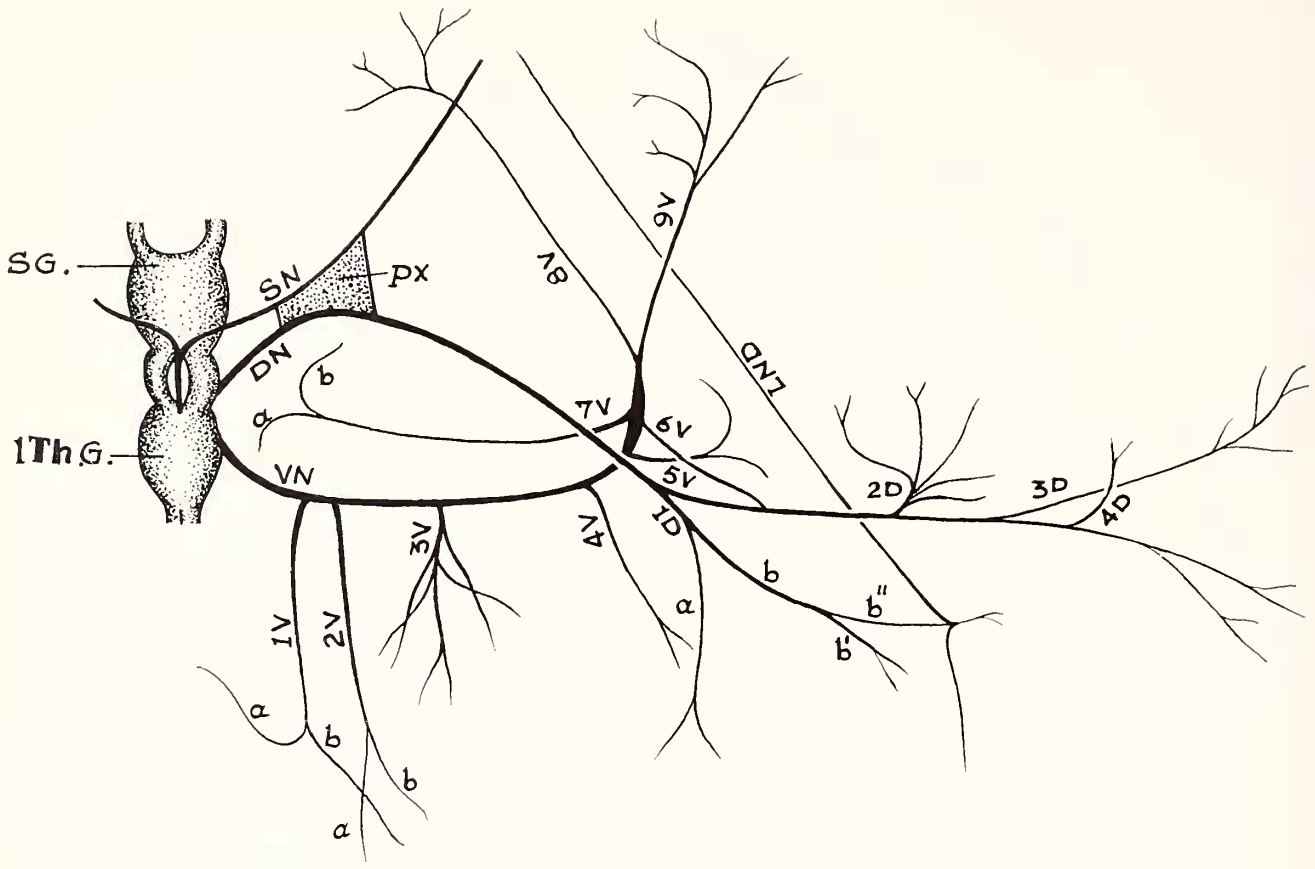

Fig. 1

FIG. 1. Diagram of the nerve pattern of the prothoracic segment of the larva of *Prodenia litura*.

mately terminates into fine branches supplying the dorsal longitudinal muscles. THE VENTRAL NERVE: The ventral nerve (VN) leaves the ganglion at the middle of the lateral margin and passes posteriorly below the ventral median muscle group and over the ventral external oblique muscles. It gives rise to a number of branches. The first branch (1V) runs obliquely downwards and bifurcates into a and b. The former passes deep into the prothoracic leg to innervate its muscles whereas the latter innervates the ventral internal and external oblique muscles. The second branch (2V) gives rise to a fine branch (a) which supplies the muscles of the leg and the other branch (b) innervates the ventral median muscle. The third branch of the ventral nerve (3V) subdivides into a number of fine branches to innervate the tracheae and ventral internal lateral muscles. The main ventral nerve after proceeding ahead for a short distance, curves anteriorly above the ventral internal lateral muscle and flattens. From the proximal part of this arises a small fourth branch (4V) which innervates the tracheae. The fifth branch (5V) innervates the tracheae and the ventral internal lateral muscles. The sixth branch (6V) extends to join the main dorsal nerve. Whereas the seventh branch (7V) proceeds as far as the prothoracic ganglion and innervates the ventral external oblique muscles, the eighth nerve (8V)

extends into the head to supply the tracheae and muscles of that region. The ninth nerve (9V) gives origin to a number of minute nerves which innervate the various ventral longitudinal and oblique muscles and tracheae of the neck and adjoining regions.

THE SUBCONNECTIVE NERVE: There is no median nerve in this ganglion so that the transverse nerves are also absent. From the mid antero-dorsal side of the prothoracic ganglion arises a single nerve which may be taken as the median nerve. It proceeds anteriorly for a very short distance and then bifurcates above the suboesophageal ganglion to give rise to a pair of the so-called subconnective nerves (SN). Each nerve passes laterally to innervate the various muscles of the head but before taking a curve, a plexus (px) is formed between it and the adjoining dorsal nerve.

NERVES OF THE MESOTHORACIC GANGLION (Fig. 2)

THE DORSAL NERVE: This nerve (DN) arises from the outer margin of the interganglionic connective, just a few millimeters above the mesothoracic ganglion. It passes laterally over the external and internal median muscles and after a short distance extends its first branch (1D) which passes over the ventral internal lateral longitudinal muscles and fuses with the transverse nerve. It, however, gives rise to a branch (a) which extends another three small branches to innervate the tracheae, ventral internal lateral muscles and the lateral internal oblique muscle.

The main dorsal nerve proceeds ahead and gives rise to another connective branch (2D) which also fuses with the transverse nerve, just posterior to the spiracle. But before fusion, it gives rise to a branch at the point c′ which proceeds antero-dorsally and divides into a number of minute branches. The branch c1 extends posteriorly to innervate the two pleurosternal oblique muscles, the branch c2 innervates the tergosternal muscle and the branches of the lateral tracheal trunk and the branches c3 and c4 proceed to innervate the dilator and occlusor muscles of the spiracle respectively. In addition to these, the branch 2D gives rise to two small branches (a and b) which innervate the lateral internal oblique and ventral external oblique muscles respectively.

The main dorsal nerve passes dorsally above the lateral longitudinal tracheal trunk and gives rise to a connective (3D) which runs to fuse with the transverse nerve. The connective gives off two minute branches posteriorly and they innervate the dorsal and lateral external oblique muscles and tracheae. The fourth branch (4D) innervates the integument and the dorsal internal lateral muscle. The main nerve, by now, becomes thin and extends ahead into the dorsal region, giving off small branches. The branches 5D, 6D and 7D innervate the dorsal external oblique muscle and dorsal internal lateral muscle group. The main nerve ultimately terminates into a number of very fine branches which innervate the tracheae and the dorsal internal median and

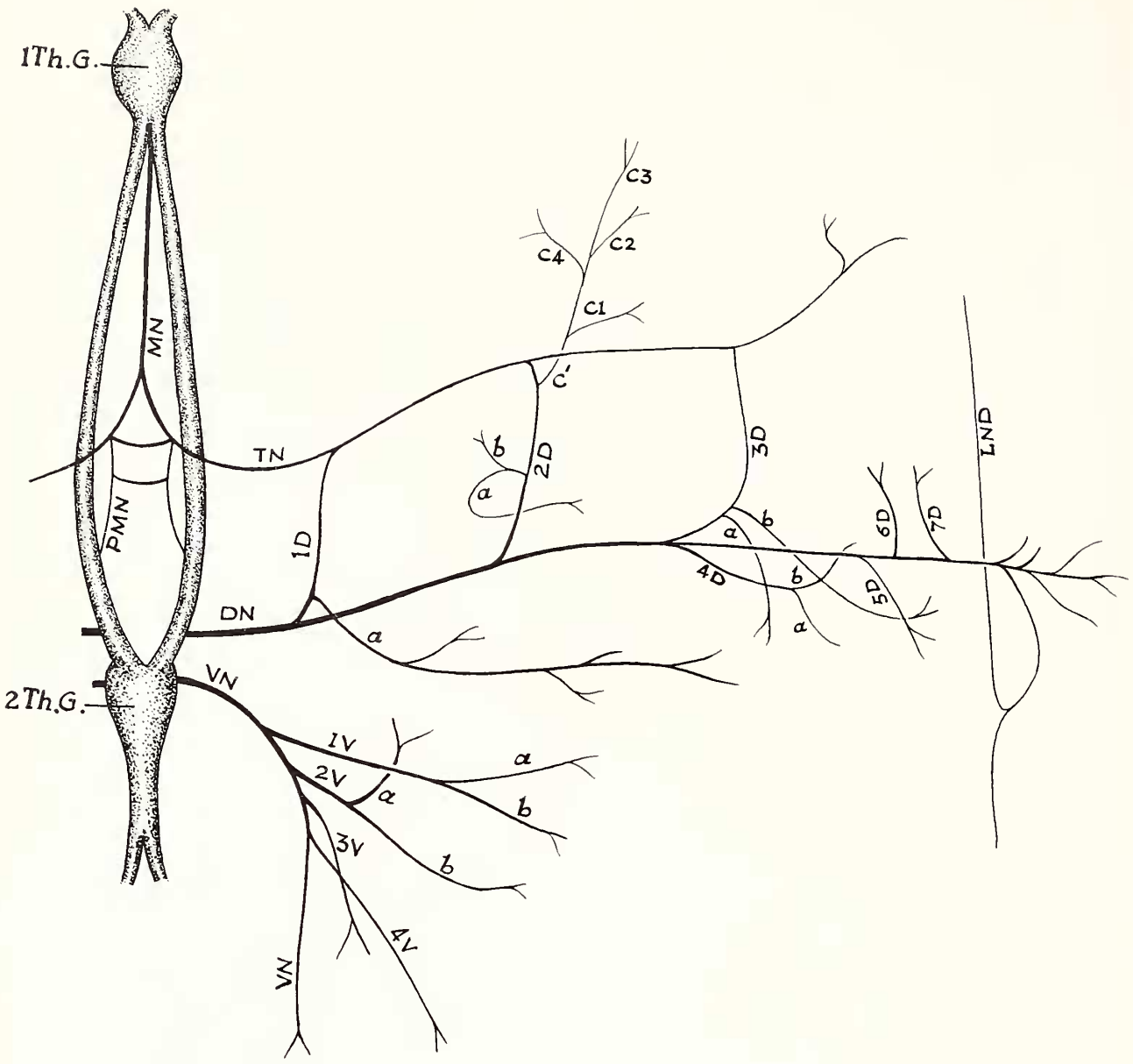

Fig. 2

FIG. 2. Diagram of the mesothoracic nerve pattern of the larva of *P. litura*.

oblique muscles. The longitudinal nerve of the dorsum (LND) is also present in between the intersegmental folds. It has its anterior attachment with the integument at the base of the dorsal internal lateral longitudinal muscles and its posterior attachment with the posterior intersegmental fold, beneath the insertion of the lateral internal oblique muscles. It remains connected to the dorsal nerve by a fine terminal branch of the dorsal nerve.

THE VENTRAL NERVE: The ventral nerve (VN) arises from the ganglion about the middle of its lateral margin and passes obliquely posteriorly over the ventral external oblique muscles. It gives rise to three branches, amongst which, the first branch (1V) extends two branches (a and b) to innervate the ventral external and lateral oblique muscles, tergosternal muscle and tracheae. The second branch (2V) bifurcates so that one branch (a) innervates the meso-

thoracic leg, ventral external oblique muscle and the integument, and the other branch (b) innervates the mesothoracic leg. Very near to the second branch, originates the third branch (3V) which innervates the ventral external and internal oblique muscles and tracheae. The fourth branch (4V) directly runs into the mesothoracic leg to innervate its muscles. The main nerve itself passes posteriorly to innervate the ventral external and internal oblique muscles.

THE TRANSVERSE NERVE: The unpaired median nerve (MN) of the mesothoracic segment arises from the fused intersegmental ganglionic connectives at the point where the connectives separate, that is, a very short distance posterior to the prothoracic ganglion. The median nerve travels about two thirds of the distance in between the interganglionic connectives and then gives off a pair of transverse nerves (TN). The transverse nerve receives three connective branches from the dorsal nerve as already stated. The two lateral connectives lie on the two sides of the lateral longitudinal tracheal trunk. The main transverse nerve which runs over this tracheal trunk, above the dorsal internal lateral muscles, terminates into the aorta to innervate it.

POSTMEDIAN NERVE: A pair of fine nerves which may be designated as the postmedian nerves (PMN) arise from the transverse nerves, very near to the point of bifurcation of the median nerve. They proceed posteriorly and meet the interganglionic connectives at two points, a little above the mesothoracic ganglion. The two nerves communicate with each other by a pair of very short connectives.

NERVES OF THE METATHORACIC GANGLION (Fig. 3)

THE DORSAL NERVE: The dorsal nerve (DN) arises from the outer margin of the interganglionic connective and passes over the ventral external oblique muscles for a short distance and then penetrates to run beneath the ventral internal lateral muscles. The first branch (1D) of the dorsal nerve extends to meet the transverse nerve but in addition gives rise to a branch (a) which subdivides into a number of minute branches to innervate the ventral external and internal oblique muscles and the ventral internal lateral longitudinal muscles. The main dorsal nerve subsequently sends off another connective branch (2D) which proceeds antero-laterally and fuses with the transverse nerve. But just near the fusion point, the branch 2D extends a branch anteriorly which innervates certain sternopleural muscles and tracheae. In addition, the branch 2D gives rise to two small branches (a and b) which innervate the lateral internal oblique and ventral external oblique muscles respectively. The third connective branch (3D) of the dorsal nerve again fuses with the transverse nerve. A side branch (a) from this nerve bifurcates to innervate the sternopleural muscles, tracheae and integument.

The main dorsal nerve then passes towards the mid-dorsal region and extends the fourth branch (4D) which passes anteriorly and then curves sharply

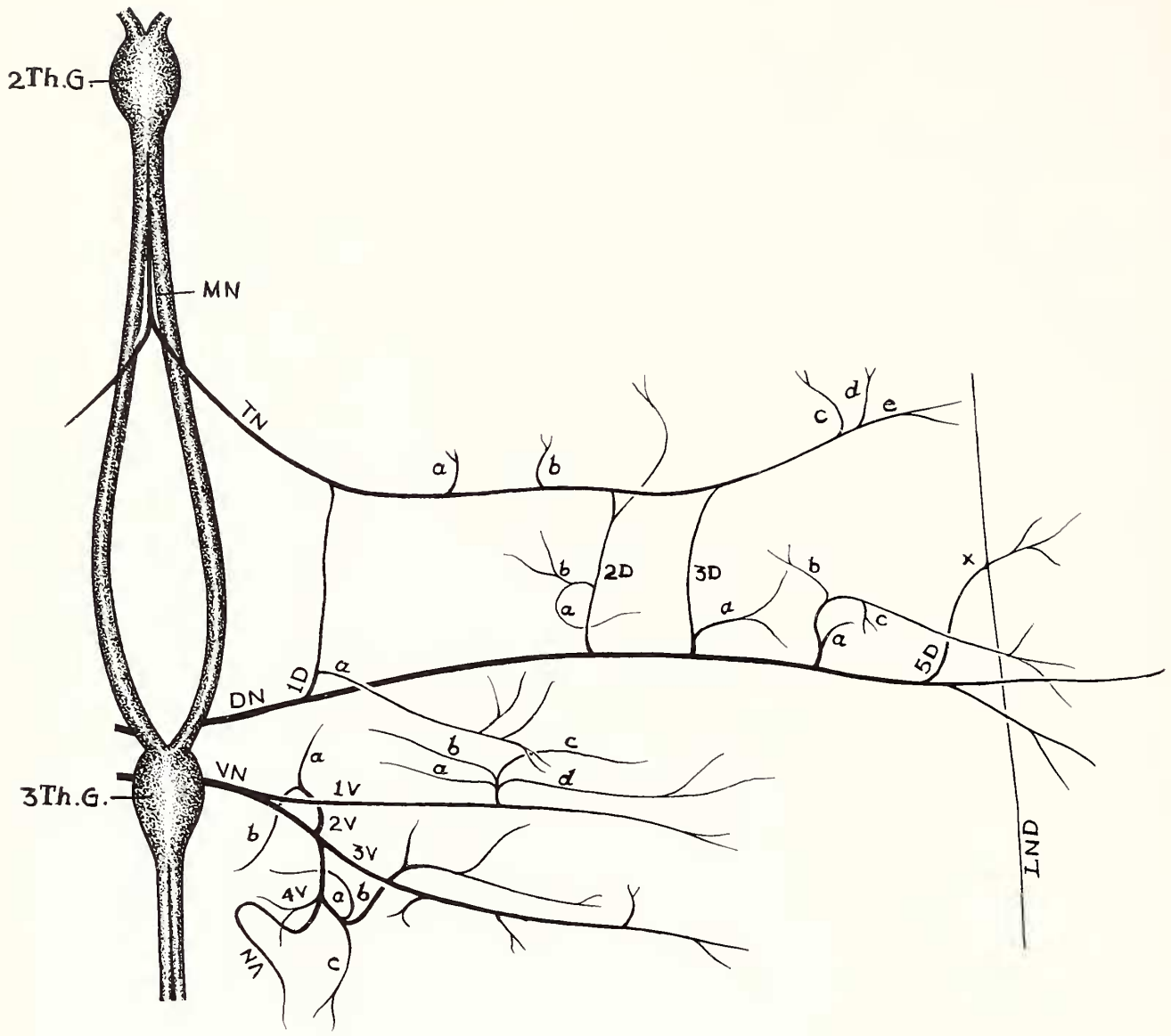

Fig. 3

FIG. 3. Diagram of the metathoracic nerve pattern of the larva of *P. litura*.

postero-dorsally, giving origin to a number of minute branches at intervals. Its first minute branch (a) innervates the paratergal muscle, the second, third and fourth branches (b, c, d) innervate the lateral internal oblique muscles and the dorsal internal lateral longitudinal muscle. The other branches innervate the various median and lateral longitudinal muscles of the dorsal region. The fifth branch (5D) of the dorsal nerve is short and fuses with the longitudinal nerve of the dorsum (LND) at the point x. The main dorsal nerve by now becomes extremely thin and fine and bifurcates into two branches which innervate the integument, dorsal internal median and dorsal external muscles.

THE VENTRAL NERVE: This nerve (VN) leaves the ganglion from the middle of its lateral margin and passes obliquely posteriorly beneath the crossed diagonal muscles and over the ventral external oblique muscles. It is com-

paratively shorter and extends into the metathoracic leg to innervate its muscles. It, however, gives rise to a number of branches during its course. The first branch (1V) runs below the ventral internal lateral muscles and gives rise to a small branch which immediately subdivides into four minute branches. Among these, the first three branches (a, b, c) innervate the integument whereas the other branch (d) passes over the lateral longitudinal tracheal trunk and bifurcates to innervate the sternopleural muscle and the integument of the dorsal region. The main branch (1V) extends further ahead over the lateral longitudinal tracheal trunk and gives rise to several small branches which innervate the lateral external oblique and tergosternal muscles and the integument.

The second branch (2V) of the ventral nerve runs anteriorly and bifurcates. Whereas one branch (a) innervates the metathoracic leg, the other (b) innervates the integument. The third branch (3V) arises near the origin of the second branch and while it proceeds laterally, it gives rise to a number of minute branches which innervate the ventral external and internal oblique muscles, sternopleural and tergopleural muscles and the integument of that region. The fourth branch (4V) penetrates into the leg to innervate it whereas the fifth branch (5V) divides into three branches. The first branch (a) innervates the leg muscles, the second (b) innervates the ventral internal median muscle, the integument and tracheae and the last branch (c) runs posteriorly to innervate the two ventral external oblique muscles.

THE TRANSVERSE NERVE: A pair of transverse nerves (TN) arises by the bifurcation of a median nerve. Each transverse nerve passes over the dorsal and ventral internal longitudinal muscles and receives three connections from the dorsal nerve as already stated. During its course, it gives rise to two very minute branches (a and b) which innervate the tracheae. Before terminating, the transverse nerve divides into three minute branches. The first two branches (c and d) pass inwards to supply certain small muscles, integument and tracheae whereas the third branch (e) passes towards the mid-dorsal region to innervate the aorta.

DISCUSSION

In the *Prodenia* larva, the thorax bears three distinct ganglia. The dorsal nerve arises directly from the prothoracic ganglion but in the meso and metathoracic segments it arises from the interganglionic connectives. Nesbitt (1941) in Orthoptera described an anterior ganglionic connective extending from one ganglion to the other. He has shown that the anterior part of the nerve may adhere to or even become incorporated in the adjoining interganglionic connective. This nerve has been termed as intercalary nerve by Pipa and Cook (1959) and Matsuda (1956) whereas dorsal nerve connective or anterior ganglionic connective by Schmitt (1959). In *Dissosteira, Acheta, Periplaneta* and *Orchelimum,* Schmitt found varying degrees of adherence to or fuse with the

adjoining interganglionic connective so that with the adherence of the anterior ganglionic connective too, the dorsal nerve seems to emerge from the connective. This condition is seen in the metathorax of *Orchelimum*. In *Prodenia* larva also the dorsal nerves in the meso and metathorax arise from the interganglionic connectives, as already stated and as such the case appears to be parallel with that of *Orchelimum*. In *Chauliodes* (Neuroptera) also Maki (1936) found a similar condition and Schmitt thinks that it is possible that the dorsal nerve in this insect is simply adhering to the nerve cord and does not lack an anterior connective but the resemblance with *Orchelimum* suggests that a dorsal nerve connective occurs in *Chauliodes* too. It must, therefore, be taken as fused. In the prothoracic segment of the *Prodenia* larva, however, the dorsal nerve arises directly from the ganglion. It appears that the proximal part of the dorsal nerve in this case has not fused with the interganglionic connective but the anterior ganglionic connective has fused with the interganglionic connective. Among other lepidopterans, Weber (1954) found an anterior connective of the dorsal nerve but Du Porte (1915) did not observe it in *Sphida* and has shown the dorsal nerve to arise from the interganglionic connective similar to the condition seen in *Prodenia* larva.

The median or unpaired nerve in the larva is a short nerve which bifurcates to form two transverse nerves of a segment. Exceptions were noted in the larva of *Papilio* by Hillemann (1933) who figured a continuous median nerve between the second and third thoracic ganglia, and the same was observed by Marquardt (1939) in *Carausius*. The origin of the prothoracic median and transverse nerves is different in the larva so that the latter have been named as the subconnective nerves. Each nerve meets the dorsal nerve through a plexus and hence on this basis it can be conveniently presumed that these nerves are actually the transverse nerves. Peterson (1912) also reported the presence of subconnective nerves in the larva of tomato worm. In *Prodenia* larva, fusion of the transverse nerve from the prothoracic ganglion with mesothoracic dorsal nerve and of the transverse nerve from the mesothoracic ganglion with the metathoracic dorsal nerve has been observed. Such fusions have also been reported in *Chauliodes, Aqulla, Perla, Carausius, Blattella, Periplaneta, Telea, Dissosteira* and *Papilio*. Most writers have designated the transverse nerve by that name but Pipa and Cook (1959) identified it simply as "nerve 8."

Whereas in the prothoracic segment, the subconnective nerve joins the dorsal nerve through a plexus, in the meso and metathoracic segments the connection between the transverse and dorsal nerves is maintained by three connectives. Du Porte (1915) also reported three such connections in *Sphida* larva but Swaine (1920) observed two or three in *Sthenopis* larva. Hillemann (1933) found two connections in the *Papilio* larva. Nothing appears to be known regarding the function of the axons which presumably pass from the transverse or subconnective nerve to the prothoracic dorsal nerve. Wittig (1955) found

that in *Perla* these transverse nerves pass to certain small dorsal longitudinal muscles and have no contact with the dorsal nerves but Schmitt (1959) reported that in *Dissosteira* the transverse nerves join the second cervical nerves and that somewhat distad of the junction, there is a connection from the second cervical nerve to the prothoracic dorsal nerve by means of which presumably axons from the transverse nerve could reach the same destination as in *Carausius* and *Chauliodes* and perhaps *Perla* also. In *Prodenia* larva the case too appears to be similar though the connection between the subconnective and prothoracic dorsal nerves is through a plexus. In the larva the transverse nerve actually terminates in the dorsal vessel and the same innervation was described by Libby (1961) in the abdomen of *Hyalophora*. In the abdomen of Orthoptera, however, Alexandrovicz (1913), Nesbitt (1941) and Schmitt (1959) found the innervation of the dorsal vessel from the dorsal nerves. The question whether there is a real difference in the innervation of the dorsal vessel in Lepidoptera and Orthoptera or the same axons are involved but follow different nerve paths appear problematic. The fact that the transverse nerve directly innervates the dorsal vessel but receives three connective branches from the dorsal nerve suggests that the dorsal vessel is innervated not only by the axons of the transverse nerve exclusively but by those of the dorsal nerve, also. This interpretation reconciles the views of orthopteran and lepidopteran workers.

In the larva of *Prodenia*, there is only one pair of thoracic spiracles lying in the prothorax. Each is innervated by a branch from the second connective joining the transverse and dorsal nerves of the mesothoracic segment. Case (1957) has shown that in the cockroach the axons to the spiracular muscle actually issue from the transverse nerve and the same was demonstrated by Hoyle (1959) in *Schistocerca gregaria*. On the basis of their findings it can be presumed that here also the axons from the transverse nerve travel into the connective branch and then into the spiracular muscle through another minor branch. The spiracular muscle also receives axons from the dorsal nerve, travelling by the same path.

It has already been pointed out that the thoracic spiracle is innervated by a branch from the connective 2D so that it may be considered to be homologous to the A–B connection present in the abdomen in Orthoptera, Plecoptera (Schmitt 1954, 1962, 1963), Lepidoptera (Libby 1959), and Neuroptera (Maki 1936).

The ventral nerve usually innervates the leg muscles, the various ventral oblique muscles and the integument. In the meso and metathorax of *Prodenia* larva there is a pair of ventral nerves in each segment. In other lepidopterous larvae also the same arrangement and number has been observed (Swaine, 1920; Hillemann, 1933; Du Porte, 1915 and Peterson, 1912). In the prothorax of the larva, the ventral nerve not only innervates the leg muscles and oblique muscles but also the muscles lying at the base of the head. In *Dis-*

sostera, Schmitt found a prothoracic nerve to join one of the cervical or ventral nerves. He further considered this prothoracic nerve to be the counter part of the dorsal nerve of the meso and metathorax. In the present case though there is no connection between the prothoracic nerve and the ventral nerve, yet there exists a connection (6V) between the dorsal and the ventral nerves. On the basis of Schmitt's interpretation, it may be concluded that it is through this connective that the axons from the dorsal nerve travel to the muscles at the base of the head.

The concept that in ancestral insect, there was a common ancestral pattern of musculature as well as innervation in each segment of the body, gets support in the present study that the nerve patterns in thorax as well as in abdomen (unpublished) of *Prodenia* larva are practically identical especially with reference to the 2D or A–B connection. This connection has been described in the abdomen of widely separated orders of insects like Orthoptera, Plecoptera (Schmitt 1954, 1962, 1963), Neuroptera (Maki, 1936), and Lepidoptera (Libby, 1959). The presence of this connection in different insect groups suggests the existence of a basic segmental nerve plan.

SUMMARY

The nerves of the thoracic segments of the larva of *Prodenia litura* have been described in detail. The thorax bears three distinct ganglia, each giving rise to three pairs of nerves which are dorsal, ventral and transverse. The dorsal nerve mainly innervates the dorsal muscles whereas the ventral nerve innervates the leg and ventral muscles. The transverse nerve mainly supplies the dorsal vessel. The dorsal nerve of the prothoracic ganglion remains connected by a plexus to the subconnective nerve which has been considered to be a transverse nerve. In the other two segments, the dorsal nerve fuses with the transverse nerve at three points by means of three connectives. In contrast to this, the ventral nerve does not fuse with the transverse nerve. The spiracular muscles are innervated from the connective lying in between the dorsal and transverse nerves. The pattern of the nerves is the same as found in other lepidopterous and orthopterous insects and that supports the concept that a basic segmental nerve pattern exists within the insects.

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KEY TO ABBREVIATIONS

DN = Dorsal nerve, LND = Longitudinal nerve of the dorsum, MN = Median nerve, PMN = Post median nerve, px = plexus, SG = Suboesophageal ganglion, SN = Subconnective nerve, TN = Transverse nerve, Th.G = Thoracic ganglion, VN = Ventral nerve.